

Cineradiographic Study of Forelimb Movements During Quadrupedal Walking in the Brown Lemur (*Eulemur fulvus*, Primates: Lemuridae)

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ABSTRACT Movements of forelimb joints and segments during walking in the brown lemur (*Eulemur fulvus*) were analyzed using cineradiography (150 frames/sec). Metric gait parameters, forelimb kinematics, and intralimb coordination are described. Calculation of contribution of segment displacements to stance propulsion shows that scapular retroversion in a fulcrum near the vertebral border causes more than 60% of propulsion. The contribution by the shoulder joint is 30%, elbow joint 5%, and wrist joint 1%. Correlation analysis was applied to reveal the interdependency between metric and kinematic parameters. Only the effective angular movement of the elbow joint during stance is speed-dependent. Movements of all other forelimb joints and segments are independent of speed and influence, mainly, linear gait parameters (stride length, stance length). Perhaps the most important result is the hitherto unknown and unexpected degree of scapular mobility. Scapular movements consist of ante-/retroversion, adduction/abduction, and scapular rotation about the longitudinal axis. Inside rotation of the scapula (60°–70°), together with flexion in the shoulder joint, mediates abduction of the humerus, which is not achieved in the shoulder joint, and is therefore strikingly different from humeral abduction in man. Movements of the shoulder joint are restricted to flexion and extension. At touch down, the shoulder joint of the brown lemur is more extended compared to that of other small mammals. The relatively long humerus and forearm, characteristic for primates, are thus effectively converted into stride length. Observed asymmetries in metric and kinematic behavior of the left and right forelimb are caused by an unequal lateral bending of the spinal column. *Am J Phys Anthropol* 111:245–262, 2000. © 2000 Wiley-Liss, Inc.

The aim of this study was to contribute to the understanding of evolutionary changes of the locomotory apparatus within the Theria (marsupials and placental mammals). Most profound changes, e.g., the decoupling of the scapula from the trunk, occurred in the shoulder of the therian stem lineage. Such decoupling resulted in new motion abilities of therians. A characteristic feature in the locomotion of small to medium-sized therians is the retroversion of the scapula

about the proximally placed instantaneous center of rotation during stance (Miller and van der Meché, 1975; Jenkins and Weijs,

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1979; Fischer, 1994). This movement alone accounts for more than two thirds of stance propulsion in various mammals (Fischer, 1998; Fischer and Lehmann, 1998; Schilling and Fischer, 1999). Furthermore, limb geometry remains surprisingly rigid throughout the stance phase. Only minor angular movements occur in the shoulder and elbow joint. The kinematics can best be described as pantograph limb (Fischer and Witte, 1998).

Within primates, humeral retraction replaces scapular retraction with increasing body size and forelimb length. Whitehead and Larson (1994) described scapular and humeral movement during walking in a vervet monkey (*Cercopithecus aethiops*). In this species, the retro- and anteversion of the scapula differ in amount of rotation and in timing from recordings in other small and medium-sized mammals (Fischer, 1998; Schilling and Fischer, 1999), and humeral movements prevail. Based on a single study, it is hard to tell whether these results represent characteristics of locomotion in quadrupedal primates in general. Small to medium-sized primates could still share a principle of the locomotion of other small mammals: crouched posture and scapular movement in a high fulcrum (Fischer, 1994). To test this hypothesis, we analyzed the movements of forelimb joints in the brown lemur (*Eulemur fulvus*), a typical arboreal quadrupedal primate of medium size (Ashton and Oxnard, 1964; Hildebrand, 1967; Napier, 1967; Rose, 1973; Walker, 1974). Arboreal quadrupedalism is regarded as the ancestral mode of locomotion in primates (Cartmill, 1972; Jenkins, 1974a).

Quadrupedal primates are also known to differ from nonprimate quadrupeds in gait patterns (Hildebrand, 1967; Vilensky, 1987, 1989) and in stride lengths (Alexander and Maloiy, 1984; Reynolds, 1987). Adult quadrupedal primates usually use diagonal-sequence, diagonal-couplets walk. Primates with such a symmetrical gait pattern can show asymmetrical behavior of the left and right limbs, particularly in the forelimbs (Hildebrand, 1967). One forelimb can take a longer stride than the other, enabled by asymmetrical bending of the spinal column. Lateral dominance and hand preferences have been frequently analyzed for nonloco-

motory movements of forelimbs in primates. Left-hand reaching preferences were proven for many prosimians (Larson et al., 1989). Surprisingly, other studies (Vilensky and Gehlsen, 1984; Demes et al., 1990) analyzed only one forelimb, probably assuming that the contralateral limb would behave in much the same way.

In this study, we compare metric and kinematic parameters of forelimb movement of the brown lemur with studies of other primates (Alexander and Maloiy, 1984; Vilensky and Gehlsen, 1984; Reynolds, 1987; Demes et al., 1990; Whitehead and Larson, 1994; Jenkins et al., 1978) and of small and medium-sized nonprimates (Jenkins, 1971, 1974a,b; Jenkins and Weijs, 1979; Fischer, 1998; Fischer and Lehmann, 1998; Schilling and Fischer, 1999). We are especially interested in whether scapular mobility is restricted in favor of an increased range of humeral movement in ancestral arboreal-quadrupedal primates, as has been observed in the vervet monkey (Whitehead and Larson, 1994) and in the spider monkey (Jenkins et al., 1978).

As all movements of proximal limb segments are hidden under the skin, fat tissue, and muscles, cineradiography was applied to study the kinematics in detail.

ANIMALS AND METHODS

One male and one female brown lemur were obtained through approved sources by our Institute. Experiments were approved by the Committee for Animal Protection of the state of Thuringia. Experiments were performed on the male brown lemur, which was trained by positive conditioning to walk on a horizontal motor-driven rope-mill, an arboreal analogue of a treadmill. Tread speed was not fixed, but held manually at a relatively constant level during X-ray shots. Only a few cineradiographic records were collected of the proximal forelimb of the female brown lemur, which walked on a flat treadmill during a preliminary X-ray session. After this session, the animal was excluded from further experiments because we diagnosed a skeletal disease (spondylosis).

Cineradiography

The X-ray equipment consists of an automatic Philipps® unit (type 9807 501800 01) with one X-ray source image intensifier chain. Pulsed X-ray shots were applied (~50 kV, 200 mA). Images were recorded using a camera (Arritechno R35-150) on 35-mm film at 150 frames/sec. The animals were filmed in a lateral projection by a maximum exposure time of 10 sec. The image intensifier has a field of 20.5×15 cm and did not allow recordings of complete forelimbs. Therefore, proximal segments (scapula, humerus) and distal segments (forearm, hand, and wrist joint) were filmed separately. An orthogonal wire grid, perpendicular to the projection plane, provided reference points for motion analysis and for correction of geometrical distortions in the sagittal plane.

Two copper wires (20 mm) superficially attached on the left upper arm and forearm made it possible to distinguish left and right forelimb and to estimate abduction and adduction angles of the humerus and forearm. As muscles of the upper arm and forearm have the form of a conical cylinder around the bones, the markers do not lie exactly parallel to the longitudinal axis of the bones. Thus, the abduction angle of the limb segment inferred from the foreshortening of markers is only an approximate value. As the distal end of humerus was frequently off the screen, the real abduction angle of the humerus could not be calculated from foreshortening of the bone in parasagittal projection. Stance and swing lengths were determined from videotapes synchronously taken with cineradiography, because they exceeded the length of the image intensifier.

Processing X-ray images

X-ray films were copied onto video tapes and analog/digital (A/D)-converted using a video processing board, and were interactively processed by the software "Unimark 3.6" (by R. Voss), which was specifically developed for this purpose. It allows the researcher to interactively digitize previously defined landmarks with a cursor function, to correct distortions automatically, and to calculate angles and distances. The positions of digitized landmarks and calcu-

lated angles in the parasagittal plane are illustrated in Figure 1a,b. Calculated angles are the projections of actual angles onto the sagittal plane, representing their contribution to movements in the plane of forward motion.

The error of landmark digitization and its influence on calculated angles were tested by repeating digitization of one sequence (~25 frames) five times. The digitization error depends on the size of the animal and the image contrast of skeletal elements. For the brown lemur, digitization error is comparatively small. It ranges from 0.3° – 0.6° for segment angles. It is roughly 1° for joint angles, because the errors of adjacent segment angles may be cumulative in joints.

Analysis of angular movements and their contribution to propulsion

Maximum amplitudes of joint excursion during stance and swing phases, and the timing of segment and limb joint movements, were calculated. Effective angular movements were defined as the difference between angles at touch down and lift off. Metric gait parameters (speed, stride duration, and stride length) were also determined. A correlation analysis was applied to reveal the interdependency between metric and kinematic parameters. The statistical significance of left/right differences in metric and kinematic parameters was tested using Student's *t*-test.

Fischer and Lehmann (1998) proposed a new approach ("overlay method") for calculating the relative contribution of angular movements to stance propulsion, considering the displacement of fulcrum of limb segments. Calculations are based on mean values of typical gait sequences, of which stance and swing phases are set in the same duration using the method of linear interpolation. Based on this method, the data of each limb segment are smoothed but their characteristics are preserved. Then, a polynomial fit of the sixth order is required to interpolate the data of the stance phase, and to increase the number of values (to about 50) in order to reduce the error factor in the following calculations. For calculation, angular values were defined against the vertical plane in such a way that they are positive if

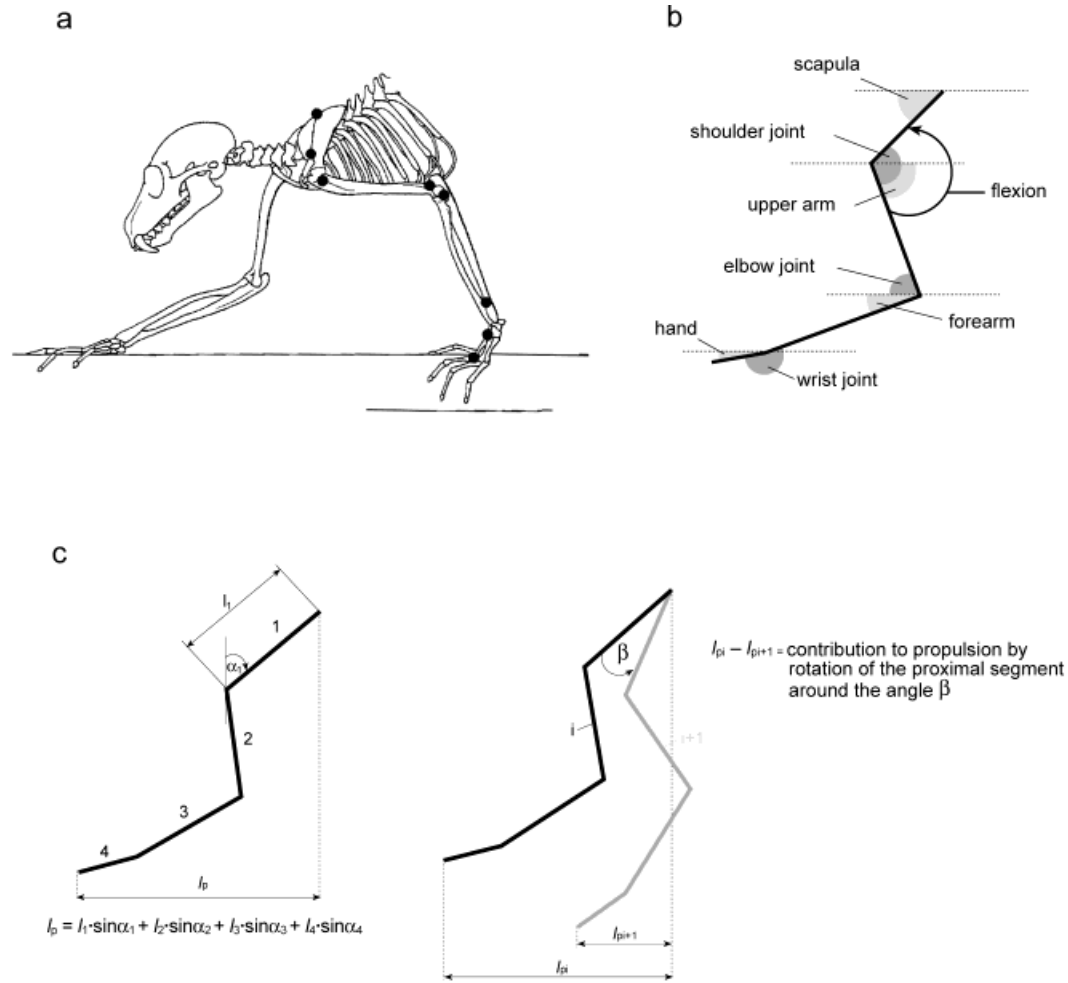


Fig. 1. Kinematic analysis. **a:** Selected skeletal landmarks. **b:** Calculated joint and segment angles. **c:** Calculation of the contribution of segment displacement to stance length.

the distal end of the segment is in front of the proximal end. The horizontal distance (l_p) between fingertip and the highest fulcrum of the limb was determined for each discrete limb configuration during stance, using the length of segments and their angular values against the vertical plane (Fig. 1c). By turning the proximal segment into the next configuration without changing angles in the more distal joints, the difference between the horizontal excursion at instant i (l_{pi}) and at instant $i + 1$ (l_{pi+1}) is the propulsion caused by rotation of this segment (Fig. 1c). The absolute contribution to stance propulsion of each segment is given

by summation of all data in stance phase. Afterwards, the contribution to forward motion of the remaining segments was calculated in the same way, but under subtraction of the angular movement, which is achieved by the rotation of the more proximal segment or segments.

Terminology

Limb joint angles were defined anatomically and measured at the flexion side of each joint. Segment angles were calculated against the horizontal plane (Fig. 1b). We use the term anteversion for the cranial displacement of the distal end of each seg-

TABLE 1. Metric gait parameters

Parameter	Left forelimb (n = 57)		Right forelimb (n = 33)		
	Mean value \pm SD	Range	Mean value \pm SD	Range	
Part 1: Complete database for male brown lemur					
Speed (m/sec)	0.83 \pm 0.22	0.46–1.45	0.94 \pm 0.20	0.58–1.61	
Stride duration (s)	0.88 \pm 0.19	0.49–1.26	0.83 \pm 0.16	0.51–1.17	
Stance duration (sec)	0.49 \pm 0.13	0.21–0.85	0.56 \pm 0.13	0.34–0.76	
Swing duration (sec)	0.39 \pm 0.11	0.17–0.63	0.27 \pm 0.09	0.13–0.52	
Stride length (m)	0.69 \pm 0.07	0.49–0.84	0.76 \pm 0.09	0.55–0.89	
Stance length (m)	0.33 \pm 0.04	0.23–0.46	0.36 \pm 0.05	0.26–0.44	
Swing length (m)	0.36 \pm 0.05	0.23–0.46	0.40 \pm 0.05	0.27–0.46	
Stride frequency (Hz)	1.20 \pm 0.28	0.79–2.04	1.25 \pm 0.26	0.85–1.96	
Part 2: Selection of strides (n = 12) with identical speeds to show the statistical significance of left/right differences					
Speed (m/sec)	0.84 \pm 0.15	0.58–1.07	0.84 \pm 0.15	0.58–1.07	
Stride duration (sec)	0.83 \pm 0.16	0.58–1.19	0.87 \pm 0.14	0.64–1.17	
Stance duration (sec)	0.47 \pm 0.12	0.34–0.76	0.54 \pm 0.10	0.44–0.71	$\Leftarrow P = 0.001$
Swing duration (sec)	0.36 \pm 0.10	0.17–0.51	0.33 \pm 0.10	0.17–0.52	$\Leftarrow P = 0.5$
Stride length (m)	0.68 \pm 0.07	0.52–0.77	0.72 \pm 0.09	0.55–0.85	$\Leftarrow P = 0.1$
Stance length (m)	0.32 \pm 0.04	0.25–0.40	0.34 \pm 0.05	0.26–0.42	$\Leftarrow P = 0.1$
Swing length (m)	0.36 \pm 0.05	0.23–0.42	0.37 \pm 0.05	0.27–0.45	
Stride frequency (Hz)	1.25 \pm 0.23	0.84–1.72	1.18 \pm 0.20	0.85–1.56	
Duty factor (%)	56 \pm 9	44–77	62 \pm 8	47–79	$\Leftarrow P = 0.001$

ment (= cranial rotation or protraction). Retroversion describes its caudal displacement (= caudal rotation or retraction). In the special case of the shoulder joint, we do not use the human-oriented terminology in which flexion in this joint refers to cranial motion of the distal humerus. In quadrupedal mammals, flexion in the shoulder joint is defined as the decrease of the caudal angle between scapula and humerus (Boczek-Funke et al., 1996; English, 1978; Goslow et al., 1981; Tokuriki, 1973). As shoulder joint movements normally consist both of humeral and scapular displacements, we cannot follow the suggestion of Whitehead and Larson (1994) to avoid the terms flexion and extension for describing shoulder joint movements. The definitions of metric and kinematic parameters are summarized in the Appendix.

RESULTS

Metric gait parameters

Metric gait parameters were available only for the male brown lemur. Speed, stride duration, and stride length were measured for a total of 90 stride cycles (Table 1, part 1). Observed speeds ranged from 0.5–1.6 m/sec. The brown lemur increases speed by increasing stride frequency. Stride duration decreases significantly ($P = 0.001$) with in-

creasing speed (Fig. 2a). Maximum stride duration (1.26 sec) was measured at minimum speed (0.46 m/sec). Reduction of stride duration results from both a decreasing stance and swing duration (Fig. 2c,e). However, the relationship between stance duration and speed is not linear. Stance duration decreases more at lower than at higher speeds (Fig. 2c).

To test the statistical significance of observed left/right differences in metric parameters, we chose some strides (n = 12) with identical walking speeds and compared the values of the left and right forelimb using Student's *t*-test (Table 1, part 2). Left and right forelimbs differ significantly in stance duration ($P = 0.001$). The right forelimb shows a relative longer stance duration (duty factor, 62%) than the left forelimb (duty factor, 56%).

Only on the left forelimb we did observe a significant increase of stride length with increasing speed ($P = 0.1$). The swing length is positively correlated with speed in both forelimbs (Fig. 2f). Stride length of the left forelimb is roughly 4 cm shorter than that of the right forelimb at the same speed (Table 1, part 2). We observed these differences under treadmill conditions but also in unrestrained locomotion. Videotape recordings of unrestrained locomotion also exist for the

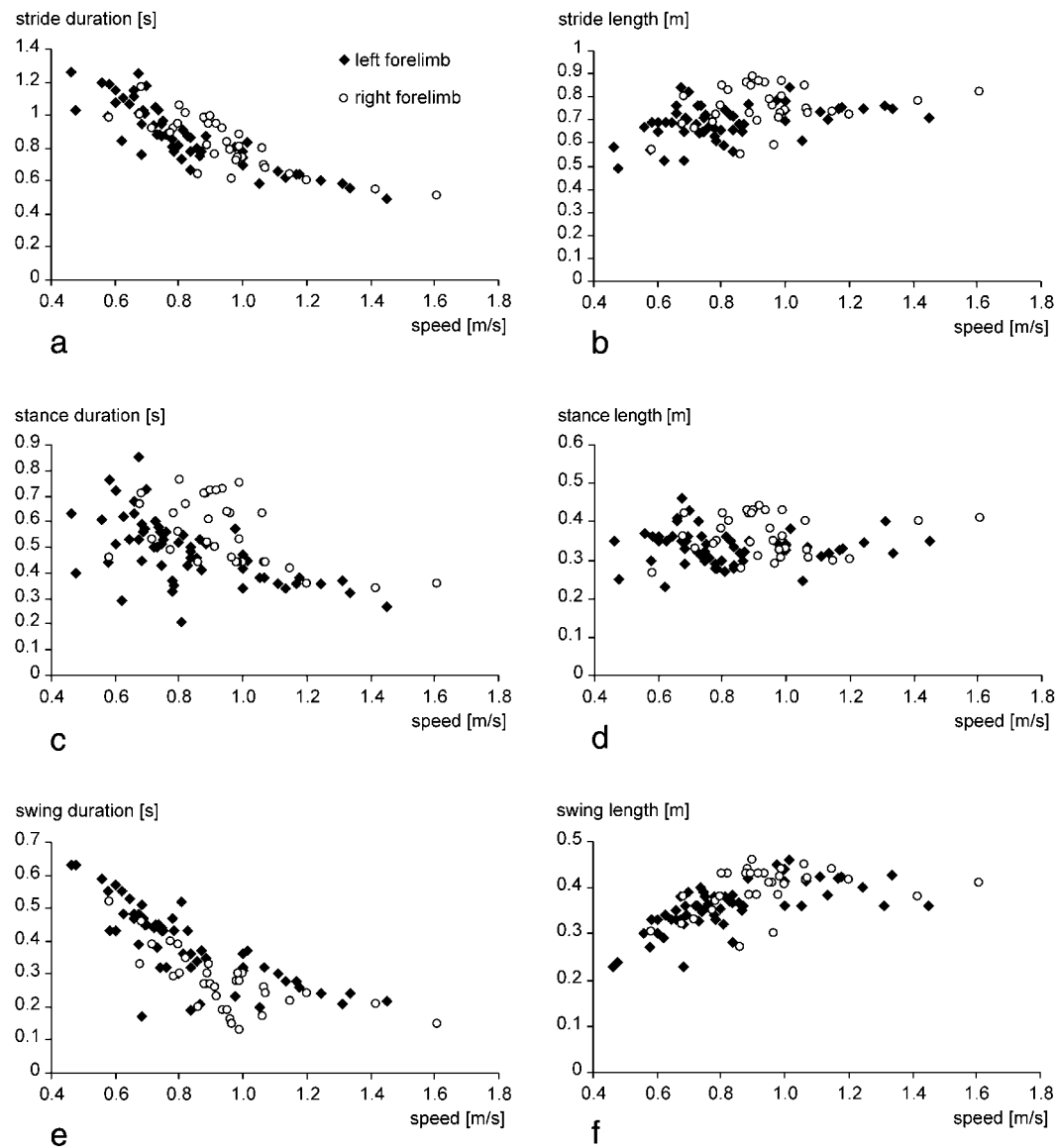


Fig. 2. Changes of metric gait parameters with increasing speed. **a:** Stride duration. **b:** Stride length. **c:** Stance duration. **d:** Stance length. **e:** Swing duration. **f:** Swing length. \blacklozenge , left forelimb; \circ , right forelimb.

female brown lemur. This animal shows no significant differences between left and right forelimb in metric gait parameters.

Kinematic study

To show that the observed differences between left and right forelimb kinematics are likely an individual eccentricity of the male brown lemur, we report the data of the

proximal forelimb kinematics of the female walking on a flat treadmill. We show some common traits, but we do not discuss the differences between these animals, which could also have been caused by the different substrate.

The description of the kinematics of the forelimb comprises the joint and segment angles at touch down and lift off, the ampli-

TABLE 2. *Statistics of kinematic parameters of the male brown lemur (during rope-mill locomotion): angle at touch down and lift off, and maximum amplitude of stance*

Angle (°)	Left forelimb			Right forelimb			Left/right differences
	n	Mean \pm SD	Range	n	Mean \pm SD	Range	
Scapula							
Touch down	66	49 \pm 3	43–56	58	47 \pm 5	31–58	
Lift off	45	82 \pm 8	56–98	37	85 \pm 8	71–100	
Amplitude	29	42 \pm 9	24–56	25	56 \pm 7	31–69	
Upper arm							
Touch down	114	126 \pm 13	86–154	82	127 \pm 10	96–14	
Lift off	78	0 \pm 8	–21–20	70	14 \pm 7	–2–33	$\Leftarrow P = 0.001$
Amplitude	55	130 \pm 17	90–158	59	131 \pm 17	81–170	$\Leftarrow P = 0.1$
Forearm							
Touch down	23	25 \pm 3	19–31	11	22 \pm 5	15–30	
Lift off	37	118 \pm 14	76–138	22	126 \pm 11	105–142	$\Leftarrow P = 0.001$
Amplitude	10	109 \pm 24	56–150				
Metacarpus							
Touch down	10	6 \pm 3	3–12	8	5 \pm 3	3–8	
Lift off	10	69 \pm 15	48–90	7	71 \pm 12	52–93	
Shoulder joint							
Touch down	62	168 \pm 11	141–186	47	167 \pm 10	145–184	
Lift off	45	78 \pm 11	57–103	35	102 \pm 7	90–124	$\Leftarrow P = 0.001$
Amplitude	27	94 \pm 15	61–130	25	71 \pm 12	47–89	$\Leftarrow P = 0.1$
Elbow joint							
Touch down	23	153 \pm 11	137–171	9	151 \pm 7	140–157	
Lift off	26	118 \pm 18	79–139	15	144 \pm 8	122–156	$\Leftarrow P = 0.001$
Amplitude	12	88 \pm 19	60–121				
Wrist joint							
Touch down	10	195 \pm 5	186–200	8	198 \pm 4	189–202	
Lift off	10	223 \pm 10	208–239	7	229 \pm 9	209–234	

tude of angular movements, and their effective contribution to linear parameters, together with the intralimb coordination of joint movements. We distinguish between retro- and anteversion of limb segments, and proper movements of joints. Segment displacement is not necessarily linked with flexion or extension in the adjacent joint but may merely follow movements initiated more proximally.

In arboreal quadrupedal locomotion, the diameter of branches is usually smaller than the diameter of the animal's trunk. The hands are placed in front of the trunk, but during stance they are positioned under the trunk. Therefore, the elbow joint is lateral to the shoulder joint, the humerus moves into an abducted position, and the forearm is adducted. Abduction and adduction angles are given separately. Joint angles are projected in the sagittal plane to give their contribution to propulsion in the direction of movement.

Three-dimensional movements of the scapula. Retroversion of the scapula (synonymous caudal rotation of Fischer, 1994; or extension in the sense of Miller and van der Meché, 1975; English, 1978; Boczek-Funcke

et al., 1996) begins at touch down at an angle of 45° ($\pm 5^\circ$), which is the minimum angle during the whole stride cycle in the majority of observations (Table 2). It ends in the last fifth of stance at an angle of about 90° ($\pm 9^\circ$). Thus, anteversion begins before lift off (Fig. 5). Consequently, maximum amplitudes are higher than the effective angular movements during the stance phase (Table 2). For the female brown lemur, the range of scapular movement during one stride cycle is comparable with the degree of scapula excursion in the male (Table 3). The scapula angles at touch down and lift off are independent of speed and stride duration. Changes in stance length are only correlated with angles at lift off ($r = 0.72$, $n = 82$, $P = 0.001$). No scapular translation along the thoracic wall could be observed. The fulcrum of retro- and anteversion is situated in the proximal third of the scapular spine, near its vertebral border.

Scapula movements of the brown lemur do not only consist of retro- and anteversion but include rotation about the longitudinal axis of the scapula to a hitherto unknown and unique degree (Fig. 3). The rotation angle is estimated by comparing scapula

TABLE 3. Statistics of kinematic parameters of the female brown lemur (during treadmill locomotion): angle at touch down and lift off, and maximum amplitude of stance of the proximal forelimb

Angle (°)	Left forelimb			Right forelimb		
	n	Mean \pm SD	Range	n	Mean \pm SD	Range
Scapula						
Touch down	15	52 \pm 4	47–58	19	51 \pm 3	44–57
Lift off	16	95 \pm 6	82–105	18	94 \pm 6	83–111
Amplitude	8	55 \pm 5	49–65	12	53 \pm 4	46–60
Upper arm						
Touch down	15	117 \pm 11	85–132	18	118 \pm 18	78–136
Lift off	17	0 \pm 5	–9–7	19	2 \pm 7	–10–17
Amplitude	9	120 \pm 9	107–135	13	119 \pm 19	74–138
Forearm						
Lift off	7	125 \pm 6	115–134	6	125 \pm 8	117–142
Shoulder joint						
Touch down	14	169 \pm 12	132–180	18	169 \pm 18	132–187
Lift off	15	94 \pm 7	83–105	18	97 \pm 7	83–109
Amplitude	8	76 \pm 7	64–84	12	77 \pm 21	34–104
Elbow joint						
Lift off	7	125 \pm 6	114–132	6	124 \pm 12	108–143

shape in the cineradiographic frame with a scapula from a dissected skeleton. The angle is given in the horizontal plane. When the angle is 0°, the scapula is in a parasagittal position. At 90° it would be parallel to the transverse plane, with the superior border facing medially. The scapula begins to rotate mediad in the middle of swing phase. At touch down, the angle of median rotation reaches a value of 60°–70°, and the scapula is laid onto the dorsal side of the thorax (Figs. 3a, 4). The scapula stays in this position until midstance. Only then does it rotate back to a parasagittal plane (Figs. 3c, 4).

During the stance phase the scapula is also abducted, with the glenoid fossa positioned lateral to the vertebral border. The abduction angle of 25°–30° remains nearly constant during stance. After lift off and during the first quarter of the swing phase, the scapula is in a roughly parasagittal position. The angle of abduction increases again to 25°–30° before touch down.

Movements in the shoulder joint. As explained previously, the shoulder joint angle is measured on the posterior side of the scapula and humerus (Fig. 1), and flexion of the shoulder joint means the diminishing of this angle. The shoulder joint displays a biphasic kinematic movement pattern during the stride cycle (Fig. 5). Flexion begins shortly before or at touch down and reaches a minimum angle when the wrist joint passes

underneath the shoulder joint. It is then followed by only a slight extension. A second flexion begins synchronously with the beginning of scapula anteversion, even before lift off. The minimum angle is reached immediately after lift off. Afterwards the shoulder joint extends continuously until the end of the swing phase.

To test the statistical significance of the left/right differences in the kinematics of the male's forelimb, we chose some strides of identical speed and compared the kinematic parameters using Student's *t*-test. Shoulder joint angle at touch down in both forelimbs has nearly the same value on the left and right side (Table 2, Fig. 5). In contrast to this, the angles at lift off are significantly different ($P = 0.001$). The right shoulder joint is more extended. The female shows no significant differences in shoulder joint movement between the left and right limb.

Correlation analysis does not show a significant linkage of shoulder joint movement with speed or stride duration. Only the left shoulder joint angle at touch down is closely correlated with stride length ($r = 0.79$, $n = 27$, $P = 0.001$). The increase of shoulder joint angle at touch down leads to an increase in stride length. Swing length depends on the extension of the shoulder joint before touch down in both extremities.

Differences between kinematic parameters of the left and right shoulder joint in the male, together with the adjoining scapu-

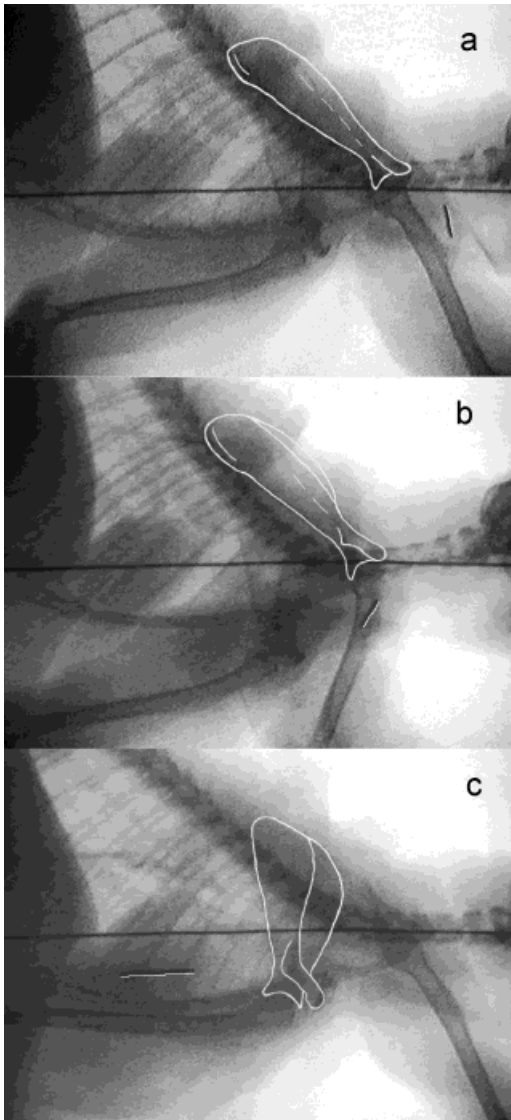


Fig. 3. Cineradiographic records. **a:** Touch down. **b:** Midstance. **c:** Lift off. Note the change of position and length of the surface marker (outlined), which indicates the median rotation and the abduction of the upper arm.

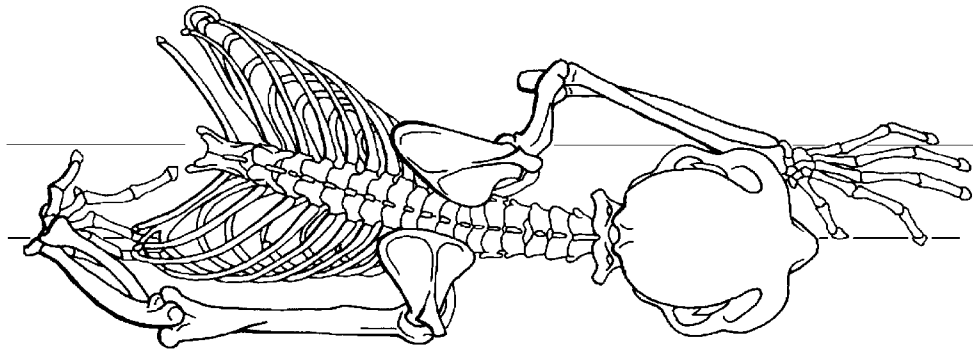
lar movements, lead to differences in the behavior of the left and right humerus. The left and right humeri are in about the same orientation at the beginning of the stance phase (Table 2). In the last quarter of the stance phase, retroversion of the right humerus ends at an angle of 17° below the horizontal (Fig. 4). The left humerus is moved more caudally and reaches a horizon-

tal position at the end of stance phase. The right humerus is also placed more horizontally when stride length increases. The described scapular anteversion before lift off is compensated for by a flexion in the shoulder joint, and the horizontal orientation of the humerus is kept. Correlation analysis indicates that the orientation of the humerus at lift off is intimately linked to stride length ($r = 0.73$, $n = 65$, $P = 0.1$). Only in a horizontal orientation may its complete length contribute to stride length. Such a horizontal position of the humerus at the end of the stance phase was also observed for the female brown lemur (Table 3).

The humerus is in an abducted orientation during stance, with a maximum abduction angle of 50° – 60° in the first quarter of the stance phase. Then a continuous decrease of humeral abduction occurs, until a minimum angle of 20° is reached at lift off. The abduction angle of the humerus increases continuously again during swing. Humeral abduction in the brown lemur is achieved strikingly differently than in man. In the brown lemur, abduction is caused by the described mediad rotation of the scapula. Whenever the scapula rotates medially and lies on the dorsal side of the thorax, the humerus follows passively, and is abducted as well as medially rotated around its longitudinal axis (Fig. 3). We never observed mediolateral movements within the shoulder joint. During locomotion the movement in this joint is restricted to flexion or extension. As the flexion/extension plane of the joint rotates medially together with the scapula, flexion of the shoulder joint in this scapular orientation results in apparent abduction of the humerus.

Elbow joint. Like the shoulder joint, the elbow joint angle has a biphasic kinematic pattern during one stride cycle (Fig. 5). The first flexion of the joint begins at touch down. Subsequent extension begins in the middle of the stance phase and reaches its maximum at lift off. After lift off, the joint is flexed and remains flexed until the last quarter of swing phase, when a second extension begins and lasts until touch down.

a



b

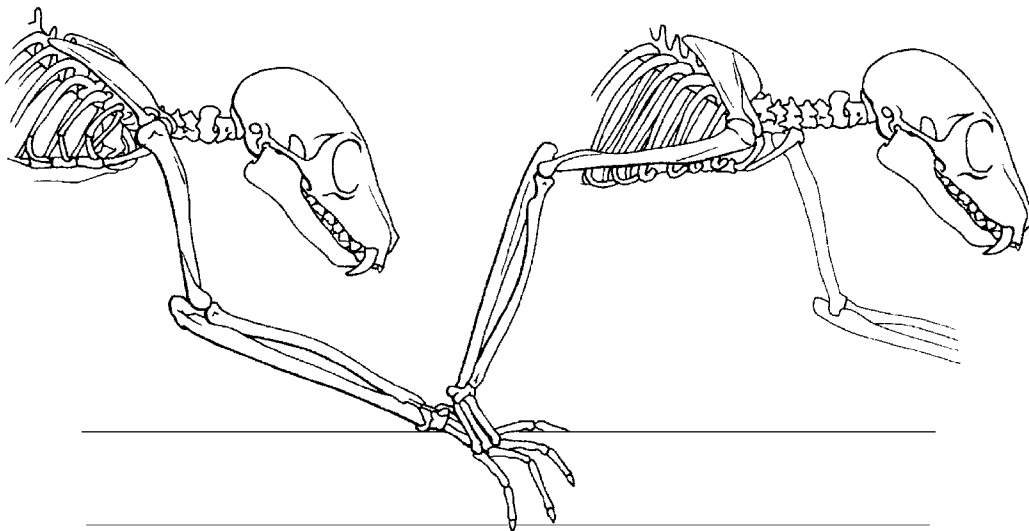


Fig. 4. Skeletal orientation of the forelimb at touch down and lift off. **a:** Dorsal aspect. **b:** Lateral aspect.

While elbow joint angles show no significant differences in both extremities at touch down (Table 2), their lift off angles are significantly different ($P = 0.001$): the right elbow joint angle is more extended. Effective angular movement of the right elbow joint is only about 7° , but it is 36° on the left. Maximum amplitude during stance is more than twice as high as effective angular movement (Table 2). Especially at the elbow joint, the differences between maximum and effective angular movement are striking. The maximum amplitude is considerably higher than the effective angular movement, point-

ing to a vertical effect. Flexion of the elbow joint during stance allows the body to move while keeping the center of gravity at a constant level between forelimbs.

Only the elbow joint shows a significant correlation between effective angular movement and speed ($r = 0.98$, $n = 12$, $P = 0.001$) or stride duration ($r = 0.89$, $n = 12$, $P = 0.001$). At increasing speed we observed an increase of effective angular movement, caused by a decreasing joint angle at lift off. A decrease in this angle also leads to a reduction in stance and swing duration, and therefore again to increasing speed. Joint

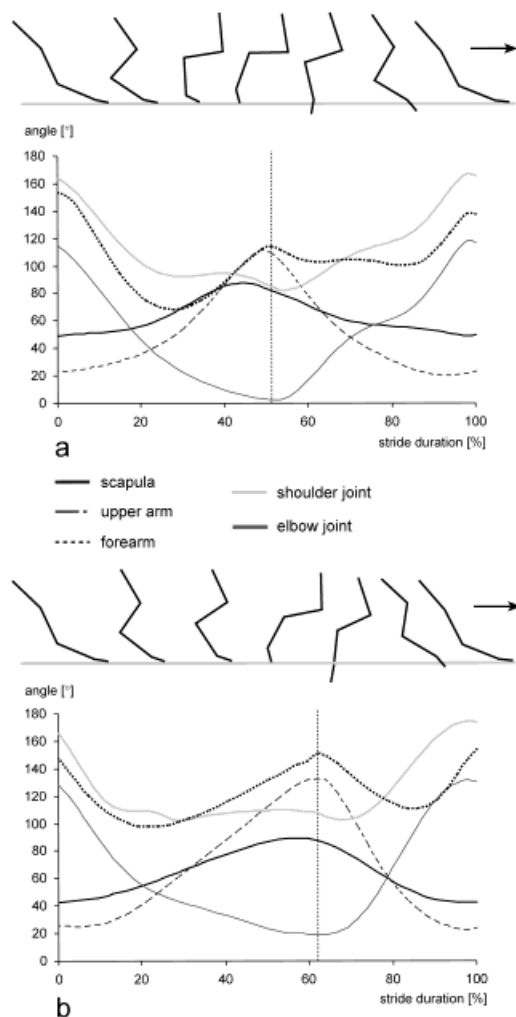


Fig. 5. Graphs of joint and segment angles of (a) left forelimb and (b) right forelimb. Stick figures illustrate the forelimb at several moments of a step cycle. The wrist joint and hand were omitted, because data are missing for the swing phase. Lift off is marked by the vertical dotted line.

angle at touch down at the end of the stride cycle is closely correlated with stride length ($r = 0.96$, $n = 9$, $P = 0.001$).

As the humerus is abducted during the stance phase, the forearm must be adducted correspondingly so that the hand may reach the branch or rope. At touch down, the adduction angle of the forearm is 30° – 33° . This angle is smaller than the humerus abduction angle, because the forearm is

about 20 mm longer than the humerus. In contrast to humeral abduction, adduction of the forearm does not decrease continually during stance. In the first third of the stance phase, the adduction angle decreases to about 22° . Adduction then ceases until the last quarter of the stance phase, before it restarts at about 80% of stance duration. The angle at lift off is approximately 18° . At this time the adduction angle of the forearm and abduction angle of the humerus are identical. While humeral abduction reaches its minimum angle at lift off, adduction of the forearm continues further. The minimum angle of approximately 13° is reached at 38% of swing. The following adduction lasts until touch down and brings the hand closer to the rope.

Wrist joint. The wrist joint angle is defined as the intersection of the forearm axis with a line between the metacarpophalangeal and carpometacarpal joints (Fig. 1b). The kinematics of the more distal hand joints (metacarpophalangeal joint, interphalangeal joints) were not considered here, because they do not contribute to propulsion in the direction of movement.

At touch down, the hand is placed in a semi-digitigrade position, at an angle of 7° to the horizontal plane. The wrist joint angle is 195° at touch down and approximately 223° at lift off. We did not observe differences in the angular movement of the left and right wrist joints.

As stance and swing lengths of one stride are longer than the diameter of the screen, we could not record the course of the wrist joint through one complete stride cycle. Therefore, we determined the effective angular movement of the stance ($=28^{\circ}$) from mean values of angles at touch down and lift off. The mean maximum amplitude is 57° .

The wrist joint angle reaches its minimum at touch down. After touch down the joint angle increases continuously up to the last quarter of the stance phase, and achieves a maximum extension of about 252° , at the moment when the wrist joint passes underneath the elbow joint. The following flexion lasts until midswing.

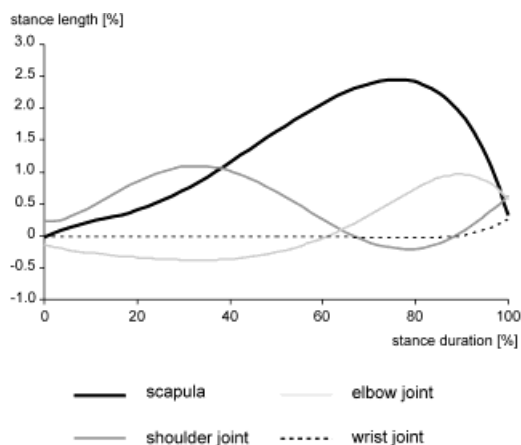


Fig. 6. Contribution of scapula anteversion and forelimb joint movement to stance length. The integral of each graph gives the absolute contribution of each joint to stance propulsion. The addition of all integrals gives the stance length. Each point within the graph indicates the instantaneous contribution at a distinct time during stance.

Contribution of segment displacement to stance length

Scapula retroversion accounts for 63% of stride length in both forelimbs. Proportions for the left shoulder joint are 31%, left elbow joint 5%, and wrist joint 1% (Fig. 6). By contrast, the right shoulder joint contributes only 23% to stride length, and the right elbow joint 13%.

The elbow joint contributes to stride length, despite the fact that the resulting joint movement of stance phase is a flexion. Flexion about a low fulcrum in the first half of the stance phase and extension about a higher fulcrum in the second half of stance lead to an overall positive contribution to stance propulsion. Shoulder joint movements cause the forward movement of the trunk in the first third of the stance phase (Fig. 6). Decreasing humeral abduction indicates scapula rotation into a parasagittal plane. Then scapula retroversion takes over the major part of stance propulsion (Fig. 6).

Intralimb coordination

Retroversion of forelimb segments (scapula, humerus, forearm) begins synchronously at touch down, in contrast to anteversion (Fig. 7a,b), which is initiated by cranial

movement of the scapula before the extremity lifts off. The forearm follows mostly at lift off. The onset of humeral anteversion varies more than that of other segments. It occurs before, at, or after lift off with equal frequency (Fig. 7b).

Maximum angles at the shoulder and elbow joints coincide with touch down (Fig. 7c). During the stance phase, the first flexion in both joints ends earlier in the elbow joint than in the shoulder joint (Fig. 7d). Elbow extension begins in 76% of cases before the onset of shoulder extension. The latter ceases until late in the stance phase, when only a slight extension can be observed. The shoulder joint will not be extended as long as the hand has not passed underneath the elbow joint. Elbow extension together with scapula retroversion maneuvers the humerus into a horizontal position.

A second flexion occurs in the elbow and shoulder joint at the end of the stance phase. Flexion of the shoulder joint always begins before lift off, and that of the elbow joint begins at lift off or shortly afterwards (Fig. 7e). The shoulder joint is flexed simultaneously with the onset of scapula anteversion. Therefore, the horizontal orientation of the humerus remains. Flexion of the elbow joint is synchronized with anteversion of the forearm.

Timing of shoulder and elbow joint movements is different during swing (Fig. 7f). During the first quarter of the swing phase, anteversion of the humerus and forearm is mainly realized by anteversion of the scapula. Additionally, the shoulder joint opens gradually, while the elbow joint keeps a more or less constant angle (Fig. 5). Up to the last quarter of swing, anteversion of the forearm is achieved only by the displacement of scapula and humerus. The elbow joint only extends at the end of the swing phase, when the humeral angle becomes greater than 90° . An extension of the elbow joint would counteract the forward movement of the limb as long as the distal end of the humerus is directed caudad.

DISCUSSION

On a treadmill, animals perform only a part of their locomotion repertoire. Tread-

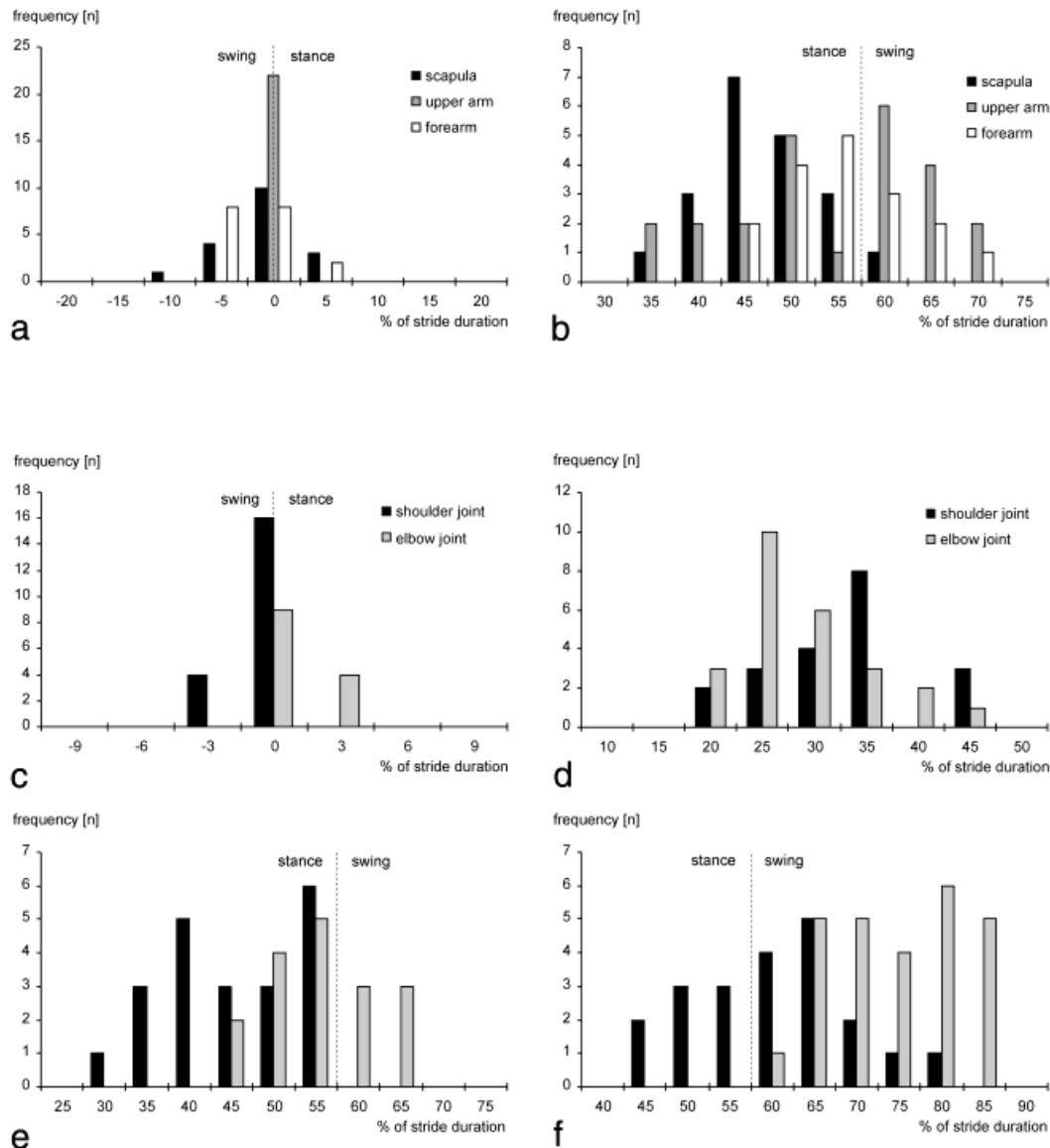


Fig. 7. Statistics of intralimb coordination of forelimb segments (a,b) and timing of shoulder and elbow joint (c-f) **a:** Onset of retroversion. **b:** Onset of anteversion. **c:** Onset of flexion I. **d:** Onset of extension I. **e:** Onset of flexion II. **f:** Onset of extension II. Note that

the retroversion of the segments is exactly synchronized and starts at touch down, just like the beginning of the first flexion in shoulder and elbow joint. The following joint and segment movements are not synchronized.

mill locomotion or restrained locomotion can be different from that on normal ground (unrestrained locomotion), as described for tree shrews (Schilling and Fischer, 1999), horses (Barrey et al., 1993), and humans (Elliott and Blanksby, 1976). Our observations on unrestrained locomotion are in

agreement with the reports on tree shrews and horses. The brown lemur shows usually higher stride lengths and lower step frequencies during treadmill locomotion as compared to unrestrained locomotion. However, only locomotion on the treadmill allows us to analyze kinematics properly using cineradi-

ography, and especially to record series of strides.

Footfall pattern and asymmetrical behavior of forelimbs

The brown lemur (*Eulemur fulvus*) performs a diagonal-sequence, diagonal-coupled walk which is typical for most quadrupedal prosimians and monkeys (Hildebrand, 1967; Vilensky, 1989). Hildebrand (1967) reported that primates with such a gait pattern may show asymmetrical behavior, particularly of the forelimbs, caused by an unequal lateral bending of the spinal column. We also found a different behavior of the left and right forelimbs in the male brown lemur in metric and kinematic parameters. Radiographic and orthopedic examination proved that the animal was in good health and showed absolutely no signs of any pathological affection of the spine or extremities.

When the animal walks on a branch or a rope, there is an undulating motion of the spine from side to side, which is achieved by an alternating lateral flexion of the spine. Such a lateral bending may help the individual to maintain balance (our personal observation); this occurs not only in lemurs but also in other arboreal-quadrupedal primates, such as the cotton-top tamarin (*Saguinus oedipus*) and the mouse lemur (*Microcebus murinus*) when walking on smaller branches. Demes et al. (1990) also reported an extensive lateral flexion of the vertebral column in lorises. The male brown lemur shows asymmetrical bending, with stronger flexion of the left side of the spinal column. This has probably developed in correlation with its distinct left-hand preference in nonlocomotory movements.

Metric gait parameters

In symmetrical gaits, there is an increase of stride frequency, and often also an increase of stride length with higher speeds in primates (Alexander and Maloiy, 1984; Vilensky and Gehlsen, 1984; Reynolds, 1987; Demes et al., 1990) and in nonprimates (Arshavskii et al., 1965; Goslow et al., 1973; Heglund and Taylor, 1988; Fischer, 1998; Fischer and Lehmann, 1998; Schilling and Fischer, 1999). Only the left forelimb of the

brown lemur shows a significant speed-related increase in stride length.

The increase of stride frequency is realized by decreasing stance and swing duration. This is also the case in slender and slow lorises (Demes et al., 1990). In rhesus monkeys (Vilensky and Gehlsen, 1984) and in nonprimates (Arshavskii et al., 1965; Goslow et al., 1973; Boczek-Funcke et al., 1996; Fischer, 1998; Schilling and Fischer, 1999), the increase of step frequency is achieved mainly by decreasing stance duration, whereas swing duration is not affected by speed.

Kinematics

Movement of the proximal forelimb.

The scapula of the brown lemur has a total retroversion of about 48°. This is markedly more than the 28° reported for the vervet monkey (Whitehead and Larson, 1994). At touch down the scapular angle is 55° in the vervet monkey, but about 45° in the brown lemur. Maximum retroversion of the scapula of vervet monkeys is also restricted to 85°, whereas the lemur scapula exceeds this value with maximum angles of approximately 95°. However, Whitehead and Larson (1994) reported a distinct scapula translation along the thoracic wall, which we did not observe in the brown lemur. Usually, such a translation occurs in acavicularian mammals (English, 1978; Boczek-Funcke et al., 1996; Fischer, 1994), but not in clavicularian therians (Jenkins, 1974b; Schilling and Fischer, 1999).

The range of scapula displacement in the brown lemur is in agreement with the results from small to medium-sized nonprimates. Schilling and Fischer (1999) reported for the tree shrew (*Tupaia glis*) a maximum amplitude of 64° for scapula retroversion in symmetrical gaits during continuous locomotion on a treadmill. The maximum amplitude given by Jenkins (1974a) for the tree shrew in exploratory walk, however, ranges only between 30°–40°. A maximum amplitude of 40°–50° is reported for the opossum (Jenkins, 1971; Jenkins and Weijs, 1979), 56° for the cui (Fischer, 1999), 40° for the cat (English, 1978; Boczek-Funcke et al., 1996), 45° for the hyrax (Fischer, 1994, 1998), and speed-dependent 33° or 42° in the pika

(Fischer and Lehmann, 1998). Jenkins (1974b) revealed a maximum scapular retroversion of 30° – 40° for the rat during exploratory walk, but Fischer (1999) observed a maximum amplitude of 55° for rats at normal walking speeds.

In the brown lemur, abduction of the scapula relative to the parasagittal plane reaches its maximum (25° – 30°) at the beginning of stance phase. The scapula is anterodorsally orientated at touch down and rotates into a parasagittal plane at the end of stance phase. The course of the rat's scapula follows the same scheme, but the angles were not quantified (Jenkins, 1974b). In the cat, abduction was determined at 12° – 17° using biplanar pulsed X-ray cinematography (Boczek-Funcke et al., 1996). The scapula of the cat remains abducted throughout the entire stride cycle.

Scapula rotation about its longitudinal axis, which is the third component of scapula movement in the brown lemur, was reported previously only for the cat (Boczek-Funcke et al., 1996). But the angle of median rotation in the cat amounts only to 4° , whereas in the brown lemur this angle normally exceeds 60° . We pointed out that this median rotation results in humeral abduction in the brown lemur, of more than 50° at the beginning of stance phase. An abducted humerus was also observed in other small and medium-sized mammals (Jenkins, 1971: tree shrew, opossum, rat, hamster, and ferret). In these animals the abduction angle of the humerus ranges between 15° – 30° . Humeral abduction in all these mammals is most probably caused by the same mechanism as in the lemur. In the cat, humeral flexion accounts for the slightly higher value for humeral abduction (10°) as compared to scapular median rotation (4°), but not to active abduction in the shoulder joint. Flexion in the shoulder joint together with a medially turned scapula leads to humeral abduction. In semiterrestrial vervet monkeys no humeral abduction was observed, and the scapula rotated only in a parasagittal plane (Whitehead and Larson, 1994). In spider monkeys (Jenkins et al., 1978), the scapula lies on the dorsal aspect of the thorax during the whole step cycle and never assumes a parasagittal position. In

contrast to quadrupedal primates, these brachiators show a higher degree of shoulder joint movements in all dimensions. In humans the scapula is also involved in humeral abduction in the transverse plane, but here most of this abduction movement occurs in the shoulder joint (Flecker, 1929; Freedman and Munro, 1966; Bagg and Forrest, 1986, 1988).

Compared to other small and medium-sized mammals, the shoulder joint of primates is more extended at touch down. The joint angle amounts to more than 160° in the brown lemur and vervet monkey (Whitehead and Larson, 1994) at the end of swing, but reaches only less than 90° in small and medium-sized nonprimates (Jenkins, 1971, 1974a,b; English, 1978; Fischer, 1994; Schilling and Fischer, 1999). The relatively long humerus and forearm in primates are, thus, effectively converted into stride length. Alexander and Maloiy (1984) suggest that adaptation for leaping would predispose primates to use longer strides during walking on the ground. But it is also plausible that for arboreal locomotion longer strides are more advantageous than higher stride frequencies at moderate walking speeds, because a stable foot position can be used longer for propulsion. Higher stride frequencies would increase the risk of a false stride. Demes et al. (1990) pointed out that high frequency gaits are disadvantageous in arboreal locomotion because they produce swinging movements of the branches that are not only dangerous but also energy-consuming.

Vertical orientation of the scapula and the horizontal orientation of the humerus at the end of stance phase occur in the brown lemur and in all small therian mammals so far studied (Jenkins, 1971, 1974a,b; English, 1978; Fischer, 1994, 1998; Fischer and Lehmann, 1998; Schilling and Fischer, 1999), except the vervet monkey (Whitehead and Larson, 1994), in which the humerus angle at lift off is about 60° below the horizontal plane.

Kinematics of the distal forelimb. Similar to the shoulder joint, the elbow joint of the brown lemur also shows an unusually high angle of about 150° at touch down. In slow lorises, the elbow joint is completely

extended and the hand touches very far ahead (Jouffroy and Stern, 1990). The elbow joint of small nonprimates is much more flexed at touch down (80° – 90°) (Jenkins, 1971; Caliebe et al., 1991; Fischer, 1994; Schilling and Fischer, 1999). In the brown lemur, the elbow joint angle is also more extended at lift off than in nonprimates with comparable body size, but the angle at touch down is still greater, and therefore effective angular movement is negative. The maximum amplitude of elbow joint movement is more than twice as much as effective angular movement during the stance phase, and indicates the function of the elbow joint as an adjusting ("fine-tuning") and stabilizing joint. This is concurrent with observations of the hyrax (Fischer, 1994, 1998), pika (Fischer and Lehmann, 1998), tree shrew (Schilling and Fischer, 1999), rat, and cui (Fischer, 1999).

Contribution of segment displacement to stance length. The calculation of the respective contribution of segment displacements to stance propulsion results in a clear division between proximal and distal parts of the forelimb. The scapular (63%) and humeral displacements (left, 31%; right, 23%) are almost solely responsible for propulsion. The elbow joint and wrist joint contribute only 6% (left forelimb) or 18% (right forelimb) to propulsion. Data on other mammals are only available for the pika (Fischer and Lehmann, 1998), the tree shrew (Schilling and Fischer, 1999), the rat, and the cui (Fischer, 1999). In the pika, the values for contribution to propulsion are: scapula, 66.5%; shoulder joint, 23%; elbow joint, 7.5%; and wrist joint, 3%; for the tree shrew in symmetrical gaits: scapula, 42%; shoulder joint, 17%; elbow joint, 32%; and wrist joint, 9%; and for the rat: scapula, 52–57%; shoulder joint, 14–21%; elbow joint, 18–25%; and wrist joint, 2–9%. The contribution of the wrist joint to stance propulsion can be neglected in the brown lemur and is even less than the already low values known for mammals without prehensile hands. Angular movements of the elbow and wrist joints serve mainly to compensate for vertical oscillations of the center of gravity caused by extrinsic factors. They are thus mostly non-

propulsive but "fine-tuning" joints (Fischer, 1994; Fischer and Witte, 1998). As described by Lemelin and Schmitt (1998), the long axis of the hand in the brown lemur is not oriented in movement direction. Hence, most of the length of this segment cannot contribute to stride length.

CONCLUSIONS

In arboreal quadrupedal locomotion, the support is usually very small compared to the size of the animal. More complex three-dimensional limb movements of an arboreal primate are achieved by a high degree of scapular mobility. It consists of ante-/retroversion, adduction/abduction, and scapular rotation about the longitudinal axis. Median rotation of the scapula, together with a flexion in the shoulder joint, mediates the abduction of the humerus, which is not achieved by a laterad segment displacement in the shoulder joint. This mode of humeral abduction is strikingly different from humeral abduction in humans. A restriction of scapular ante-/retroversion in favor of an increasing range of humeral movement, as observed for the vervet monkey (Whitehead and Larson, 1994), is not a characteristic feature of primate locomotion in general. In the brown lemur, the length of humerus and forearm is converted into stride length by a more extended shoulder and elbow joint angle at touch down as compared to nonprimates.

The calculation of the contribution of segment displacement to stance propulsion shows that scapular retroversion in a fulcrum near the vertebral border causes more than 60% of the propulsion. Forelimb joints are flexed during locomotion. An operational division between the proximal and the distal forelimb segments, as has been observed for other small mammals, may also be recognized in the brown lemur.

Movements of most forelimb joints and segments are speed-independent and influence mainly linear gait parameters (stride length, stance length). Only the effective angular movement of the elbow joint increases with increasing speed and stride frequency.

The observed asymmetries of the left and right forelimb kinematics in the male brown

lemur show that hand preferences, which are distinct in nonlocomotory actions, can also have an effect on locomotion.

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APPENDIX

Definitions

Touch down/lift off of foot

Touch down is defined as the instant in which the limb takes up the trunk load (=hard contact). *Lift off* is defined as the lift off of the metacarpus and the loosening of the grip around the rope of the treadmill.

Metric gait parameters

Stride cycle: Period from touch down to the next touch down of the same limb; only stance and swing phases are distinguished.

Stride duration (sec): Time between two successive touch downs of the same limb.

Stride length (m): Under treadmill conditions, stride length is calculated as the sum of stance and swing lengths because the trunk is not moved.

Speed (m/sec): Quotient of stride length and step duration.

Stance duration (sec): Time between touch down and lift off of a foot.

Stance length (m): Horizontal distance which is traveled by the fingertips on the treadmill during stance phase. Stance length corresponds to stance propulsion of the trunk during unrestrained locomotion.

Swing duration (sec): Time between lift off and touch down.

Swing length (m): Horizontal distance which is traveled from the fingertips during swing phase.

Kinematics

Angles of segments are given between the longitudinal axis of segment and the horizontal plane. Joint angles were measured at the flexion side of joints (Fig. 1b).

Maximum amplitude: Absolute value of the difference between the maximum and the minimum joint angle during stance or swing.

Effective angular movement: Absolute value of the difference between joint angles or segment angles at touch down and lift off.

Abduction/adduction: In human anatomy, the terms "abduction" and "adduction" are defined as displacement of a limb segment in the frontal plane. Likewise, the terms describe the positions which result from such movements. Here, these terms are used differently, to describe all positions of a limb segment in which a distal joint is located laterally or medially to the more proximal joint, as well as the movements leading to these orientations.

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